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How Ecosystems Respond to Stress

Common properties of arid and aquatic systems

David J. Rapport and Walter G. Whitford

Nearly all ecosystems are subject to periodic disturbances by natural events, such as flood, fire, drought, and insect infestation (Vogl 1980). When such perturbations are extreme, ecosystems of immense complexity undergo rapid transformation to systems of remarkable simplicity that are characterized by a scarcity of life forms and few or no symbiotic interactions. However, this transformation sets the stage for recovery, which allows the ecosystem to adapt to changing environments (Holling 1986). In healthy systems, therefore, these perturbations are seldom more than a temporary setback, and recovery is generally rapid (Odum 1969). By contrast to natural disturbances, anthropogenic stress is not a revitalizing agent, but a debilitating one. Stressed ecosystems do not recover; rather, further degradation may follow. Indeed, Odum et al. (1979) defined stress as a debilitating agent and perturbation (subsidy) as potentially beneficial.

Highly degraded ecosystems do not "bounce back" once stress loads are lessened

Anthropogenic stresses are of many specific types, but they can be classified into four main groups: physical restructuring (e.g., changes resulting from land use); the introduction of exotic species; discharge of toxic substances to air, land, and water; and overharvesting. Ecosystems lack the capacity to adapt to these stresses and maintain their normal functions and structure. Thus, stress results in a process of degradation, which is commonly marked by such signs as less biodiversity, reduced primary and secondary production, and lowered resilience (i.e., the capacity of an ecosystem to recover to its original state) to natural perturbations (Barrett and Rosenberg 1981, Odum 1985, Mageau et al. 1995).

Given that regional ecosystems are unique and thus may differ considerably in their normal ranges of primary and secondary productivity, species composition, diversity, and nutrient cycling, and given that each system is exposed to unique combinations of stresses, it might be expected that patterns of response to stresses will be highly variable and unpredictable. Therefore, it is surprising to discover remarkable similarities in the response of ecosystems to stress (Odum 1985, Rapport et al. 1985, Rapport and Regier 1995). Stressed ecosystems are characterized by a "distress syndrome" (Rapport et al. 1985) that is indicated not only by reduced biodiversity and altered primary and secondary productivity but also by increased disease prevalence, reduced efficiency of nutrient cycling, increased dominance of exotic species, and increased dominance by smaller, shorter-lived opportunistic species. These signs have been well documented in a number of studies of both terrestrial and aquatic systems (Hildén and Rapport 1993, Rapport et al. 1995, Whitford 1995, Epstein and Rapport 1996, Wichert and Rapport 1998). How might this distress syndrome pattern be explained? By what mechanisms do stressed ecosystems become degraded? Why has it proven so difficult to rehabilitate stressed ecosystems, even after the initial stresses have been reduced or removed altogether? In this article, we address these and related questions by an empirical examination of three very different regional ecosystems, each of which has had a long history of exposure to multiple anthropogenic and natural stresses.

Case study areas

We selected study areas based on three main criteria: our familiarity with the history of these regions, the extensive documentation of both stress pressures and responses over a relatively long period of time, and the contrasting nature of the structure and function of these systems.

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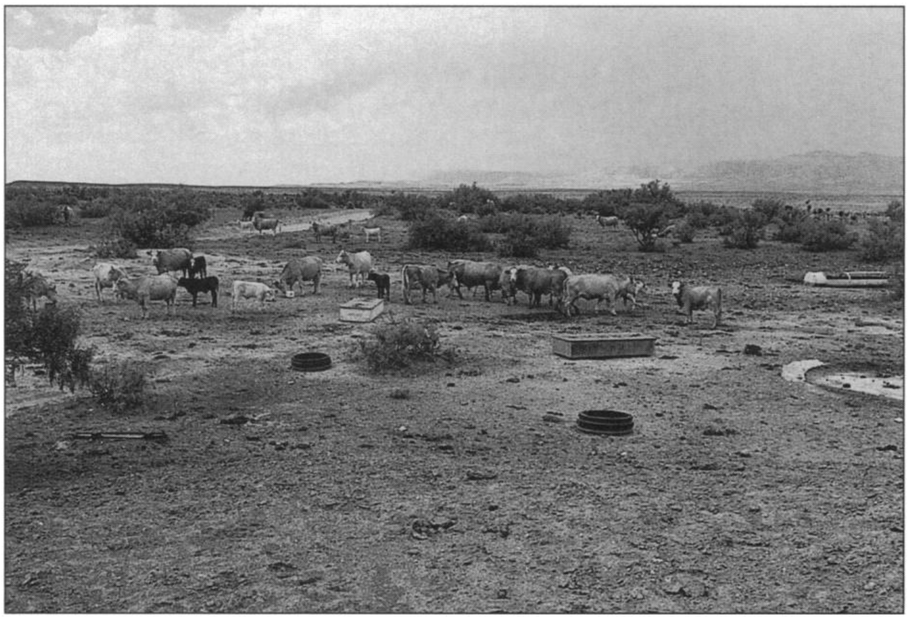

Figure 1. Increased degradation at cattle watering points in the Jornada Rangelands of the southwestern United States.

Analysis of such case studies could be carried out at many levels of organization, ranging from communities to ecosystems, landscapes, and entire regions; our analysis covers this broad spectrum but focuses primarily on the ecosystem level.

The Laurentian Great Lakes Basin. Before intensive European settlement in the early nineteenth century, the Laurentian Great Lakes Basin was characterized by extensive primary forests and by high abundance and diversity of mammals, fish, and waterfowl (Regier and Baskerville 1986). The fertile soils of the basin were ideal for agriculture. With rich soils, abundant supplies of wood, high-quality ore, and seemingly unlimited potential for power generation from many rivers and tributaries, the area was destined to become the industrial heartland of North America. By the mid-nineteenth century, the basin supported a thriving commercial fishery. Initially, the fishery used the abundant stocks of large nearshore benthic species, particularly sturgeon (*Acipenser fulvescens*) and whitefish (*Coregonus* sp.), both of which were overharvested and subsequently became locally extinct (Regier and Hartman 1973).

Figure 2. Natural, undisturbed semi-arid grasslands in the Jornada Rangelands of the southwestern United States.

Over the course of nearly two centuries of European settlement, most of the original forest cover in the southern portion of the basin (i.e., Lakes Erie and Ontario) has been replaced by extensive agricultural, urban, and industrial development. Many bays and harbors throughout the Great Lakes have been designated by the International Joint Commission on Boundary Waters (IJC) as "Areas of Concern." These areas are characterized by heavy burdens of toxic substances, impoverished natural habitats, low biodiversity, and high nutrient loads (Harris et al. 1988, Hartig and Thomas 1988). There are 131 globally imperiled species and natural communities in the Great Lakes Basin (SOLEC 1996).

Desert grasslands. The desert grasslands of North America have a long history of human occupancy (Bahre and Shelton 1993). However, degradation of these semi-arid grasslands was coincident with the development of commercial cattle ranching and the availability of well-drilling technology. The first records of major shrub and tree invasion appear after the drought of 1891–1893—a drought so severe that between 50 and 75% of the cattle in southeastern Arizona died of thirst and starvation (Bahre and Shelton 1993). By 1900, the devastating effects of overstocking were clearly recognized by government scientists (Griffiths 1901). At the present time, wind and water erosion due to overgrazing have changed vegetation patterns, erosion has led to the redistribution of soil to distant parts of the landscape, and soil compaction is common in the vicinity of livestock watering points (Figure 1). Recent evaluation of satellite imagery has documented the fragmentation of the grasslands that has followed shrub invasion and desertification (Eve and Peters 1996). Indigenous desert grasslands (Figure 2) in North America now persist only as remnant patches within a matrix of shrublands, coppice dunes, and shrub–grass mo-

Table 1. Similarities and differences in stress pressures implicated in the transformation and degradation of three different ecosystems.

Stress pressure	Laurentian Great Lakes Basin	North American desert grasslands[a]	Kyrönjoki River and Estuary
Physical restructuring	Wetland drainage; removal of shoals; dredging of harbors; removal of shoreline vegetation; canals; regulation of flows; damming of rivers	Redistribution of topsoil; loss of soil silt fraction; dune formation; arroyo formation; channel cutting	Dikes; drainage of acidic clays; damming of channels; clearing of rapids; drainage of peatlands; lowering of lakes
Overharvesting	Overharvesting of most commercial fish species; biological extinction of many stocks	Overgrazing by cattle	Risk of overharvesting of some estaurine fish
Waste residuals	Toxic substances from industrial discharge; runoff from agriculture; sewage	Livestock wastes affecting ephemeral lakes and perennial streams	Runoff from agriculture; sewage
Introduction of exotic species	Sea lamprey, alewife, and rainbow smelt displace native species; Pacific salmon introduced to deal with exotic species; accidental introduction of zebra mussels	Lehmann lovegrass, tumbleweed, African rue all displacing native grama grasses; gemsbok (oryx) and cattle displaced pronghorn antelope	No introduced species affect the ecosystem

[a]Includes ephemeral lakes and perennial streams.

saics (Whitford 1995). These shrub-dominated ecosystems represent alternate stable states compared to the original desert grasslands (Whitford et al. 1995).

The Kyrönjoki River and Estuary of southwestern Finland. The Kyrönjoki River flows into the Gulf of Bothnia (Baltic Sea), where it forms an estuary surrounded by an archipelago. Because it is a medium-sized river with a large catchment area (approximately 5000 km^2), discharge shows a large seasonal fluctuation (between 4.8 and 329 m^3/s; Hildén and Rapport 1993). As a result of more than four centuries of cultural stress, this system has become progressively degraded. A major factor contributing to ecological degradation is extensive physical restructuring in the catchment area, which includes loss of wetland habitat and nutrient enrichment (eutrophication) due to runoff from farming and human settlements (Hildén and Rapport 1993).

The sulfide-bearing clay soils are one of the most distinctive features of the Kyrönjoki River and Estuary. These soils, which cover almost 10% of the total catchment area, generally lie no more than 50 m above sea level (Erviö 1975). Runoff from the sulfide-bearing clays is highly acidic (pH less than 5; Hartikainen and Ylihalla 1986). With increases in both soil disturbance and runoff, some areas in the lower reaches of the river and the estuary have become acidified, either seasonally or permanently. The increased frequency of acid and toxic discharges to the lower and middle reaches of the river since the early nineteenth century has resulted in many large-scale fish kills (Alasaarela and Heinonen 1984). Extensive losses of salmonid habitat as a result of physical restructuring of the river basin have also contributed to the transformation of the fish community (Hildén et al. 1982).

Common stress pressures

Table 1 identifies four generic classes of human-caused stress that are implicated in the degradation of one or more of the case study ecosystems: physical restructuring, waste residuals, overharvesting, and introduction of exotic species. All four classes were active in the transformation of the Laurentian Lower Great Lakes Basin and the desert grasslands of the southwestern United States and Mexico, and three of the four classes were involved in the transformation of the Kyrönjoki River and Estuary.

Physical restructuring. Physical restructuring fragments or destroys critical habitat, causes substrate instability, and disrupts nutrient cycling. In the Laurentian Great Lakes Basin, physical restructuring has altered the nearshore area. From the mid- to late 1800s, the Great Lakes Basin was logged extensively, eliminating entire forest ecosystems. The result was stream bank erosion and severe runoff, which degraded downstream fish spawning habitats. Wetlands drainage for both agriculture and human settlement increased sediment and nutrient flows (Harris et al. 1988). The construction and dredging of harbors to facilitate shipping and the installation of artificial shoreline structures to prevent erosion (a process called "shoreline armoring") further reduced the amount of shoreline habitat. Waterfalls were dynamited to permit better passage for logs, destroying fish habitat; in some areas, including southern Lake Michigan, whole dunes were mined for sand, resulting in the elimination of dune and swale habitat (SOLEC 1996).

In the nineteenth century, dams were a common feature of most tributaries; in addition, large water-control projects, such as the Welland Canal, opened up the Great Lakes to major shipping. Constructed in 1830, the Welland Canal is approximately 27 miles long, with seven large locks capable of lifting or lowering ships a total of approximately 100 m. Whereas dams impeded the migration of fish into tributaries, canals facilitated the invasion of introduced species, such as the sea lamprey (*Petromyzon marinus*), into the Upper Great Lakes, where they have

Figure 3. A landscape dominated by mesquite (*Prosopis glandulosa*) represents an alternate stable state over the indigenous grasslands in the Jornada Rangelands of the southwestern United States.

become major problems (Regier and Hartman 1973). For example, the sea lamprey has, through predation, taken a heavy toll on the native benthic fish community, including lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), and burbot (*Lota lota*).

In the desert grasslands of North America, well-drilling and earth-moving equipment were among the earliest sources of human intervention because many of the larger desert grassland basins were devoid of perennial surface water and could not be used for livestock production until deep wells were dug to supply water for livestock. In addition, water storage tanks were dug in ephemeral lake basins, and dams were constructed on lower reaches of ephemeral streams to provide reliable sources of water for cattle. Livestock watering points were separated by as little as 2–3 km. These watering points still serve as foci for cattle, especially during the hot summer months. The concentration of livestock at wells and watering points created concentric areas of high trampling disturbance, which diminished in intensity with increasing distance from the well.

Physical restructuring also occurred as three or more species of shrubs and small trees expanded from their original, limited habitat and cover to dominate extensive areas of the desert grassland (Hastings and Turner 1965, Bahre and Shelton 1993). Shrub establishment contributes directly to changes in landscape hydrology (Martinez-Meza and Whitford 1996). Shrubs also contribute to the demise of grasses through their effects on rainfall distribution and by competition for soil water through their spatially extensive root systems.

In the Kyrönjoki River and Estuary, extensive physical restructuring has accompanied human settlement for more than four centuries. In the sixteenth century, the clearing and surface draining of land along rivers for agriculture followed the expansion of tar production. Subsequent changes have included the building of dikes; the damming of channels; the drainage of acidic clays, wetlands, peatlands, and lakes; the clearing of rapids; dredging; the lowering of lakes; the creation of artificial lakes; and flow regulation in the upper reaches of the river (Hildén and Rapport 1993). Collectively, these changes have significantly altered the natural hydrology of both the river and the estuary, eliminating critical fish and waterfowl habitat and reducing water quality.

Overharvesting. Stocks of preferred species are obviously reduced as a result of harvesting; in addition, overharvesting reduces biodiversity and facilitates the invasion of opportunistic species. Overharvesting has had the most pronounced impacts in the Laurentian Great Lakes Basin and the desert grasslands; its effects in the Kyrönjoki River and Estuary appear to be of far less significance.

In the Great Lakes Basin, overfishing has virtually decimated populations of highly valued native nearshore and benthic fishes, notably whitefish, ciscos, and sturgeon. These effects have been facilitated by other factors, such as pollution, channeling, nutrient enrichment, and predation by the invasive sea lamprey (Regier and Baskerville 1986, Regier et al. 1988).

In North American desert grasslands, overstocking cattle has led to overharvesting of native grass species (Figure 3). Overgrazing by cattle has two major repercussions: it alters soil surfaces, exposing soils so that they become more prone to wind and water erosion, and it reduces the abundance of the native flora, especially the longer-lived perennial grasses. Forage species preferentially browsed by cattle have, over the years, been replaced by woody shrubs and other grass species less palatable to cattle (Bahre and Shelton 1993), leading to degradation of the rangeland.

Waste residuals. Discharge from industrial and agricultural activities is a major source of stress in aquatic ecosystems, but it has had a more limited role in the transformation of terrestrial ecosystems such as desert grasslands. In the Laurentian Great Lakes, waste residuals from agricultural runoff, sewage discharge, and industrial emissions to air and water have contributed to widespread eutrophication of nearshore areas (Harris et al. 1988) and to the buildup of toxic substances in food webs. Fish advisories warn consumers against frequent consumption of large fish caught in the Great Lakes because of the human health risks of the persistent organic compounds that have bioaccumulated in the fish. In addition, waterfowl reproduction in the Great Lakes region has been affected by high levels of DDT and its breakdown product, DDE. The IJC Water Quality Board has identified 11 critical pollutants, including

DDT and DDE, in the Great Lakes Basin (Colborn et al. 1990).

In North American desert grasslands, animal dung transported from watersheds by overland flow becomes concentrated in ephemeral lake basins. Grazing removes virtually all of the grass cover from lake basins, leaving a barren surface with scattered dung pats. When a grazed ephemeral lake basin fills after rain, there is intense competition among the ephemeral fauna for the detritus-based food resources (Loring et al. 1988). The abundance and succession of this fauna is different in ungrazed, grass-filled ephemeral basins than it is in nutrient-enriched grazed ephemeral basins.

In the Kyrönjoki River and Estuary, regions of permanent and seasonal acidification have resulted from human disturbance to naturally occurring sulfide-containing soils, as mentioned above. Sewage discharge from human settlements and nutrient-laden runoff from agricultural lands results in eutrophication in the estuary and nearshore areas.

Introduction of exotic species. The spread of non-native species has been particularly important in changing the ecology of the Great Lakes Basin and the desert grasslands of North America. In the Laurentian Great Lakes, the accidental introduction of alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), combined with the simultaneous overharvesting of natural predators, such as the lake trout, has led to a virtual "takeover" of the original fish community by exotic pelagic species. In an attempt to control the situation and to provide a base for the sport fishery, yet another non-native species, the Pacific salmon (*Oncorhynchus* spp.), was introduced. This species filled a niche left vacant by the extirpation of larger piscivores (e.g., native trout species; Leach 1995).

The accidental spread of the sea lamprey and the introduction of the zebra mussel (*Dreissena polymorpha*) have led to further degradation of the Great Lakes Basin (Colborn et al. 1990). The sea lamprey contributed to the demise of the deepwater benthic fish community by preying on lake trout, whitefish, and burbot. Consequently, it helped shift the balance in the fish associations in the lakes from a natural, benthic-dominated fish community to an artificial, pelagic-dominated fish community. The zebra mussel, by filtering phytoplankton and zooplankton, has helped to restore the lakes to a benthic-dominant community, with low fish production. However, the reversal to dominance by an artifical benthic community has been to such an excessive degree that preferred bottom-oriented species cannot recover.

Lehmann lovegrass (*Eragrostis lehmanniana*) from southern Africa was purposefully introduced to the desert grasslands of North America in 1932 in an attempt to reseed degraded rangelands and road cuts. This experiment was overly "successful," because by 1940 Lehmann lovegrass began to appear in unplanted regions of Arizona and New Mexico (Cox et al. 1984). By 1986, this species was dominant on approximately 146,000 ha of grassland and former grassland in southeastern Arizona (Cox and Ruyle 1986, Anable et al. 1992). Large patches of lovegrass have also been seen in the rangelands of southern New Mexico. Although this grass has served admirably to prevent further erosion, thus fulfilling the initial purpose for which it was introduced, in many regions it has displaced the native black grama grass (*Bouteloua eriopoda*), lowering overall range quality (Whitford 1995).

Invasives have been less of a problem in the Kyrönjoki River and Estuary. For example, crayfish (*Astacus astacus*) was introduced into the Kyrönjoki River, probably toward the end of the nineteenth century (Pursiainen et al. 1984). The effects are not known for certain, but there do not appear to have been any dramatic impacts because after the decline of the crayfish populations (which has occurred), no significant alteration of the ecosystem has been detected.

Extreme natural events. Although not shown in Table 1, extreme natural events also serve as a stress, especially when acting synergistically with anthropogenic sources of stress. Storm events in the Laurentian Great Lakes Basin, for example, increase nutrient loading from agricultural runoff, and extreme water-level fluctuations tend to exacerbate the extent of shoreline habitat lost due to physical restructuring. In the Kyrönjoki River and Estuary, heavy precipitation events increase runoff from oxidized soils, elevating the acidity of the system. In the desert grasslands of North America, periodic drought exacerbates an already stressed system by increasing soil exposure and loss through wind erosion.

Thresholds and transformations

Several models account for the transformation of ecosystems under stress. Some involve slow, linear responses, others involve thresholds, and still others combine thresholds and nonlinear responses (Holling 1986, Patten and Costanza 1997). It is the latter model, in which stress triggers changes from one semi-stable state to another, that most closely describes the behavior of the Laurentian Great Lakes and the desert grasslands of North America. In these two ecosystems, the obvious manifestations of transformation (i.e., species decline and changes in species dominance and nutrient conditions) appeared in a relatively short time frame (over a period of 10–20 years), although the mechanisms promoting these changes were in place decades earlier. Changes in the Kyrönjoki River and Estuary, by contrast to the other two ecosystems discussed in this article, have a longer history and appear to have taken place more gradually (Hildén and Rapport 1993). In all three ecosystems, however, transformations were the result of multiple and interactive stresses, in which anthropogenic stresses acted synergistically with natural perturbations (Regier and Hartman 1973, Hildén and Rapport 1993, Whitford et al. 1995).

Transformation within the Laurentian Great Lakes Basin (and, in fact, in whole basins of the lower lakes and some bays and harbors of the upper lakes), exhibited sudden shifts from one domain of stability to another, in which the originally dominant native long-lived (and predominantly benthic) species were replaced by exotic short-lived (and predominantly pelagic) species. The transformation from a mature, integrated fish community to a largely disorganized assemblage involved the

Table 2. Main tendencies in the etiology of ecosystem breakdown.

General tendency	Laurentian Great Lakes Basin	North American desert grasslands	Kyrönjoki River and Estuary
Progressive dominance by opportunistic species	Increased dominance of short-lived exotic pelagic species over long-lived native benthic species	Replacement of long-lived dominant grasses with short-lived dominant grasses	Increased dominance of smaller, early maturing species (e.g., roach, *Rutilus rutilus*; bleak, *Alburnus alburnus*)
Progressive invasion of non-local or non-native species	Wide dispersal of exotic introduced species	Wide dispersal of non-native grass species and selection of unpalatable and drought-resistant shrubs	Not evident in this system
Shift in community structure	Shift from benthic-dominated to pelagic-dominated community; breakdown of fish associations (e.g., salmonids, percid and centrarchid waterfowl, and fur bearers)	Shift from grasslands to shrub community; increased cover of short-lived perennial grasses; replacement of grasses by shrubs	Shift from salmonids to cyprinids, except where strongly acidified; progressive loss of fish species dependent on turbulent, deeper, more stagnant water (e.g., crayfish, brook trout, and sea trout)
Loss of substrate stability	Scouring and erosion of substrate	Increase in bare patches between plants; formation of mesquite dunes in degraded rangelands	Loss of clean, washed stable sediments
Disruption of nutrient cycling	Loss of spawning and feeding grounds for dominant nearshore fish species; increase in nutrient leakiness	Loss of secondary productivity	Loss of estuarine spawning and feeding grounds for dominant coastal fish species
Progressive loss of ecosystem services	Loss of valued commercial services	Loss of virtually all livestock grazing, fisheries, recreational uses, water quality, and near-shore wildlife	Loss of valued fisheries (e.g., salmonids, burbot [*Lota lota*], and river crayfish); decline in water quality; increase in heavy metals

demise or severe reduction in lake sturgeon, lake herring (*Coregonus artedii*), lake trout, and burbot and the buildup of an exotic pelagic fishery dominated numerically by rainbow smelt and alewife.

This transformation of the Great Lakes Basin appears to be due, not to a single stress, but rather to the cumulative impact of multiple stresses, including harvesting pressure, habitat degradation, eutrophication, and the introduction of exotic fishes (Regier and Baskerville 1986, Regier and Kay 1996, Kay and Regier in press). Bays, harbors, and shoals that once served as centers of organization (i.e., locations of highly structured and integrated habitat that provide feeding and breeding grounds for the keystone species that organize the larger system) now serve as centers of disorganization. These areas have become sources of lakewide circulation of contaminated waters and sediments.

In the desert grasslands of North America, periodic drought, which is characteristic of the region, has served to exacerbate the impacts of high-density stocking, increasing the speed at which grasslands have been transformed to shrublands (Bahre and Shelton 1993, Whitford 1995). Mesquite (*Prosopis glandulosa*) and creosote bush (*Larrea tridentata*), both highly resistant to drought, replaced the once dominant black grama grass (Figure 3). Once shrub establishment and grass cover reduction has passed some threshold, a degradation trajectory is apparently followed in which the shrub community takes over at accelerating rates, even if grazing pressure is excluded (Whitford 1995). This shrub community has proven highly resilient, and efforts to restore grazing lands have been largely unsuccessful thus far (Roundy and Biedenbender 1995). After such transformations, large areas of grasslands in the Southwest that once supported indigenous grassland specialists are no longer able to support more than a small fraction of the commercially viable cattle herds that were present when ranching operations began (Griffiths 1901).

The more gradual transformation of the Kyrönjoki River and its estuary from an oligotrophic system favoring salmonids, baltic herring (*Clupea harengus*), smelt (*Osmerus eperlandus*), whitefish, and bream (*Abramis brama*) to a eutrophic system characterized by the increased dominance of pelagic fish has been less dramatic than the transformations in the two other systems. However, here, too, there has been a marked and protracted change in the direction of a simplified ecosystem that has persisted for decades and has negatively affected fish communities over the entire coastal region (Hildén and Rapport 1993). The main tendencies for ecosystem breakdown that characterize the three case studies, shown in Table 2, are consistent with the hypotheses that Odum (1985) proposed about trends that are expected in stressed ecosystems, and with the signs of ecosystem distress advanced by Rapport et al. (1985).

Mechanisms of transformation

The transformation of the three ecosystems from healthy to degraded states involved three primary mechanisms: disruption of nutrient cycling, adaptive strategies by opportunistic or exotic species, and destabilization of substrates. These mechanisms are intimately interrelated.

Disruption of nutrient cycling. Stress results in a disruption of the pattern of nutrient cycling, shifting it from a predominantly vertical direction (i.e., between biota and substrate) in healthy systems to a predominantly horizontal direction in stressed systems. In the Great Lakes, for example, degradation of nearshore vegetation enhanced the horizontal flow of nutrients so that nutrients loaded from the land were transported more readily offshore instead of being sequestered and used by nearshore vegetation.

In North American desert grasslands, stress affected nutrient cycling by decoupling primary production from rainfall and thus creating a patchy distribution of nutrient-rich and nutrient-starved substrates. In healthy desert grasslands, nutrient mineralization (the release of nutrients to the soil solution) increases with the amount of rainfall, and the distribution of nutrients is relatively uniform over the soil surface. However, in stressed grasslands that have been converted to shrublands, nutrient cycling is altered both temporally and spatially. Temporal changes result from the creation of pulses of organic matter released to the soil following seasonal rains and ephemeral plant production. These pulses result in temporary nutrient immobilization as soil microbial biomass rapidly increases in response to the sudden supply of available carbon, thus decoupling net primary production from rainfall (Whitford et al. 1987). Spatial changes in nutrient availability are another consequence of the conversion of grassland to shrubland. Shrubs create "islands of fertility" under shrub canopies in which organic matter is recycled, again in a horizontal direction, by the interactions of grazers, plants, and microbes. Outside the canopy, by contrast, nutrients are depleted in the absence of significant vegetation and the presence of soil erosion (Schlesinger et al. 1990).

In the Kyrönjoki River and Estuary, the spatial pattern of nutrient cycling also changed. In particular, the loss of riverbed vegetation facilitated lateral transport of nutrients from agricultural runoff to the phytoplankton and benthic microalgae components of the system.

Adaptive strategies by opportunistic or introduced species. Opportunistic species that were previously present but rare often become dominant in stressed ecosystems, as do exotic species, whether their introduction was accidental or deliberate. Because interactions between species have been disrupted (e.g., by natural predation or symbiotic interactions), ecosystem integrity is weakened, thereby giving rise to dominance by opportunistic and exotic species. These species are characterized by high reproductive rates, relatively short life cycles, and small size.

In the Laurentian Great Lakes Basin, for example, a pelagic fish community largely comprising introduced species has become dominant over the once abundant and highly integrated benthic fish community (Rapport 1983, Regier et al. 1988, Regier and Kay 1996). And the initial stages of degradation in North American desert grasslands are characterized by a reduction in palatable long-lived perennial grasses and an increase in short-lived perennial grasses. The short-lived grasses produce large quantities of small seeds that are readily dispersed by wind and water. Intermediate stages of degradation are characterized by the replacement of drought-resistant, long-lived perennial grasses, such as the dominant black grama grass, with short-lived grasses that are drought susceptible, such as *Aristida* spp. During drought, the loss of these grasses produces large unvegetated spaces that are susceptible to wind and water erosion. Final stages of degradation are characterized by the invasion of shrubs and the subsequent loss of virtually all livestock grazing potential, with large and exposed patches of the soil surface highly susceptible to further erosion (Grover and Musick 1990). These changes have virtually eliminated the interdependent community of the once-thriving grassland specialists, including the banner-tailed kangaroo rat and the pronghorn antelope.

In the Kyrönjoki River and Estuary, several cyprinids, especially roach (*Rutilus rutilus*) and bleak (*Alburnus alburnus*), are favored by the more eutrophic water. In the channels, the once extensive macrophytic riverbed vegetation has been replaced by phytoplankton or benthic microalgae.

Destabilization of substrates. An important mechanism facilitating the transformation from highly integrated to loosely associated communities is the loss of substrate stability. In the Great Lakes, dredging and removal of shoreline vegetation has eliminated the original community associations and their substrates. The loss of wetlands has been particularly critical because such areas support high species diversity (Jude and Pappas 1992). Their demise has caused sharp reductions in spawning grounds for nearshore fish species and localized losses of northern pike (*Esox lucius*) and walleye (*Stizostedion vitreum*; Jude and Pappas 1992).

In the desert grasslands of North America, the loss of vegetative cover has contributed to altered surface characteristics that increase the erosion potential, thus further contributing to the loss of biotic organization. The loss of substrate stability has an especially pronounced impact on the desert grasslands, where loss of soils and plant cover increases susceptibility to wind and water erosion. Eventually, erosion leads to mobile sand dunes that can degrade adjacent areas by burying vegetation.

Soil drainage for agricultural purposes has also caused groundwater levels to fluctuate, leading to oxidation and leaching of acidifying substances (Palko 1994). The acidic drainage water is then discharged directly into the river or estuary. Because the reserves of acidifying and other toxic substances in the soils are large, the river water and the estuary will run the risk of periodically experiencing detrimentally acidic conditions for as long as the sulfide clay soils are used for agriculture (i.e., for the foreseeable future). The unstable and acidic sediments entering the river and estuary has affected critical habitat for dominant coastal species, such as migrating salmonids, pike, and perch (Hildén and Rapport 1993).

Ecosystem resistance to rehabilitation

Restoring the damaged ecosystems discussed in this article will require inactivating the mechanisms that have promoted ecosystem degradation. However, once the system has transformed (i.e., once it has become degraded), the very mechanisms that have contributed to the transformation tend to perpetuate it. In the Great Lakes, for example, the disappearance of critical shoreline habitat, along with the entrenchment of non-native fauna, means that the once dominant communities in this ecosystem are not readily reestablished. These shoreline changes contribute to offshore transport of nutrients, and these nutrients in turn continue to favor the shorter-lived, non-native pelagic fish communities at the expense of the longer-lived, native-dominated benthic fish communities. Similarly, in North American desert grasslands, overgrazing has resulted in the loss of much of the native black grama grass. Restoring these highly palatable grasses has proven difficult because the loss of grass cover has exposed the soils, which have thus become more vulnerable to erosion and even less suitable for the reestablishment of vegetation. Finally, in the Kyrönjoki River and Estuary, ongoing drainage of sulfide clay soils continues to maintain an acidic environment that favors continued dominance by acid-tolerant, non-native opportunistic species and precludes the return of the native species.

Indeed, for each of the case study areas discussed in this article, there have been efforts to reverse the degradation and restore ecosystem health. However, these efforts have, by and large, not succeeded in restoring a degraded (pathological) system to a healthy condition, although success stories have been reported for other stress-damaged ecosystems (e.g., pinyon–juniper woodlands in the semiarid West, which seem to be recovering to their pregrazing, savanna-like condition; Yorks et al. 1994).

In the Great Lakes, restoration and rehabilitation have been goals for decades, particularly in the so-called Areas of Concern (Hartig and Thomas 1988)—that is, the most highly degraded bays, harbors, and estuaries. However, this highly degraded, multistressed ecosystem has proved refractory to efforts to restore healthy conditions (Colborn et al. 1990).

It is important to note that efforts to rehabilitate the Laurentian Great Lakes have not been completely ineffective; however, they have been very limited. The reduction in nutrient loading due to the control of phosphate in laundry detergents is arguably a success story: It has improved nutrient status (i.e., reduced eutrophication) in some areas (e.g., the western basin of Lake Erie and the Bay of Quinte in Lake Ontario), and fish stocks characteristic of more mesotrophic conditions have begun to recover. However, many other stresses, particularly the loading of toxic substances (many of which are now transported by atmospheric deposition) and the destruction of sensitive habitats, especially wetlands and shorelines, continue nearly unabated. Moreover, the loss of habitat, especially wetlands, precludes the reestablishment of the key fish and wildlife communities that would play a major role in the recovery of the Laurentian Great Lakes.

Another sign of limited success in the rehabilitation of the Great Lakes is that where local efforts have been greatest over the past decade—in the seriously damaged Areas of Concern—results have been insufficient to warrant "delisting" for any of these areas. Most, if not all, remain severely degraded. The biggest success story—the partial recovery of the fishery in the Bay of Quinte (Lake Ontario)—was directly attributable to the reduction of phosphates. Because wetland habitat was relatively undamaged and the primary source of stress was nutrient loading, there has been a partial recovery of walleye stocks, an important component of the original fish assemblage (IJC 1996).

Efforts at rehabilitation in the desert grasslands of the Southwest have met with less success, even though in many areas the main stress—overgrazing—has been sharply reduced. In addition, there have been some dramatic interventions, including extreme attempts at shrub removal and restoration of grasses by bulldozer leveling of coppice dunes, root plowing, and herbicide applications. However, these efforts have failed to eliminate shrubs for extended periods of time (Herbel 1983).

This lack of recovery of North American desert grasslands suggests that a self-reinforcing process comes into play as a consequence of the initial invasion of the shrubs (Roundy and Biedenbender 1995). With invasion, "resource islands" are created underneath the shrubs, as discussed previously, that create conditions for further desertification by denying nutrients to areas outside the shrub canopy. This effect leads in turn to bare patches that foster further erosion by wind and water. The shrublands are also well adapted to natural perturbations, further reinforcing their existence. In experiments in which creosote bushes were subjected to complete elimination of summer rainfall for 5 consecutive years, the drought-stressed plants not only recovered but produced new growth equivalent to that of unstressed controls within 1 month after a large rain following the removal of the "rain-out" shelter cover (Whitford et al. 1995).

In addition, the original desert grasslands were governed by the integrity of the soils that support black grama grasses. Damage to these soils (compaction and exposure), largely as a result of overgrazing, opened up unvegetated spaces, which were more vulnerable to wind and soil erosion, providing space for invading shrubs. Soil erosion now appears to have led to a positive feedback system that maintains desertification (Grover and Musick 1990).

Rehabilitation efforts in the Kyrönjoki River and Estuary are too new to evaluate the likely degree of success. However, as long as reserves of acidifying and other toxic substances remain in the soils and agriculture dominates land use, it is likely that runoff from acidic clays will continue to acidify the river and estuary.

The lessons from these experiences with efforts to rehabilitate severely damaged ecosystems are clear: Contrary to popular belief, highly degraded ecosystems do not "bounce back" once stress loads are lessened. They do not bounce back even with an "assist" from heroic efforts to restructure the system and create an artificial habitat. These findings suggest that too much effort has been expended in trying to regulate the system, instead of the human activities that stress and transform the system (Rapport and Regier 1995, Rapport et al. 1997).

Although there are many possible reasons for the lack of success in rehabilitating severely damaged ecosystems (Rapport and Regier 1995, Rapport et al. 1997), some common elements emerge from the case studies discussed in this article. First, damaged systems become more vulnerable to invasion from opportunistic species, which hinder, if not completely block, the reestablishment of the original biotic communities. Second, disturbances to substrates (i.e., soils and sediments) severely limit the possibilities for reestablishing highly organized biotic communities, which depend on complex structures and on stable substrates. Third, the disruption of nutrient cycling changes the entire character of the ecosystem, making its transformation to a system that resembles the initial conditions exceedingly difficult.

In short, all three mechanisms that were implicated in the degradation of the case study areas are also implicated in their resistance to rehabilitation. This combination of interacting mechanisms constitutes formidable barriers to the reversal of degradation. Key to the restoration of damaged ecosystems, therefore, is effectively countering the mechanisms that initially promoted and then reinforced these transformations. For example, to counter the disruption in nutrient cycling, one would need to restore substrate stability and vegetation in the desert grasslands. Similarly, restoring nutrient cycling in the Laurentian Great Lakes requires altering agriculture practices (to reduce diffuse nutrient loading) as well as restoring shoreline habitat to prevent offshore nutrient transport.

Table 3. Evidence for Ecosystem Distress Syndrome in three ecosystems.[a]

System property	Laurentian Great Lakes	North American desert grasslands	Kyrönjoki River and Estuary
Primary productivity[b]	+	0/–[c]	+
Horizontal nutrient transport	+	+	+
Species diversity[d]	–	+/–[e]	–
Disease prevalence[f]	+	+	+
Population regulation[g]	–	–	–
Reversal of succession	+	+	+
Metastability[h]	–	–	–
Community structure			
r-selected species[i]	+	+	+
Short-lived species	+	+	+
Smaller biota	+	Unknown	+
Exotic species	+	+	+
Extinction of habitat specialists	Unknown	+	+
Mutualistic interactions	–	–	–
Boundary linearity	+	+	+

[a]Reprinted from Rapport et al. 1998b.
[b]"+" indicates that the property increases in the stressed ecosystem; "–" indicates that the property decreases in the stressed ecosystem; "0" indicates that the property is unchanged.
[c]In the Jornada Rangelands of the southwestern United States, the productivity initially is unchanged as stress intensifies and then decreases with further intensification.
[d]In the Jornada Rangelands of the southwestern United States, species diversity initially increases with stress in avian fauna and small mammals due to the habitat provided by shrub layers, but species diversity of grasses and annual plants decreases. In the Great Lakes, diversity in fish and aquatic vegetation declines. In the Kyrönjoki River and Estuary, diversity in fish and aquatic vegetation declines.
[e]In the Jornada Rangelands of the southwestern United States, species diversity in birds and mammals initially increases as stress intensifies but then decreases with further intensification.
[f]Disease prevalence has been monitored in mistletoe (Jornada Rangelands), fish tumors and fish parasites (Great Lakes), and crayfish (Kyrönjoki).
[g]Population regulation declines in fishes for the aquatic systems and in grasses for the Jornada Rangelands.
[h]Local stability and resilience of dominant biotic communities.
[i]r-selected species dominate in disturbed ecosystems, particularly within the grasses of the Jornada and the fish communities of aquatic systems.

Conclusion

Half a century ago, Aldo Leopold suggested the notion of "land sickness," referring to the breakdown of regional terrestrial (and aquatic) ecosystems to whole landscapes by human activities. He drew attention to specific signs (e.g., erosion, loss of soil fertility, hydrological abnormalities, occasional irruption of certain species, mysterious local extinction of others, and qualitative deterioration in farm and forest products) by which this condition might be recognized. Today, these signs characterize not only the Wisconsin woodland on which Leopold based his work but also the conditions found in ecosystems worldwide (Rapport et al. 1995, Rapport et al. 1998a, 1998b).

The ecosystem distress syndrome (Rapport et al. 1985), which shares many features with Leopold's signs of "land sickness" (Rapport and Regier 1995), points to several factors as characteristic of degraded ecosystems: reductions in primary and secondary productivity, loss of biodiversity, disruption and leakage in nutrient cycling, and shift in dominance of biota from the larger, longer-lived life forms that are specialists in their food requirements to smaller, shorter-lived forms that are generalists (Table 3). These signs have also generally characterized the three case studies discussed in this article.

The overarching conclusion from an examination of these three cases is that the mechanisms that promote degradation can, after a certain point, set in motion a self-reinforcing system that creates further degradation even after the stresses that set the transformation in motion are withdrawn. Once entrained, these mechanisms—including disruption of nutrient cycling, adaptive strategies of opportunistic species, and instability of substrates—become both a cause and a consequence of degradation and render efforts at rehabilitation extremely problematic. Ecosystems in alternate stable, transformed states may be highly resistant to further alteration. Efforts to rehabilitate these altered ecosystems need to take into account their original state and the mechanisms responsible for the transformation. But although this approach might boost the success of rehabilitation efforts, the most effective way to ensure healthy ecosystems is to undertake preventive measures to limit stress pressures so that self-reinforcing degradative processes are not set in motion.

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